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Wing Measurements for Differentiating Three Cryptic Species of *Myotis* (Mammalia: Chiroptera) that Co-occur in the Southeastern United States

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Abstract

Identification of cryptic species often relies on invasive techniques such as comparison of cranial morphology or generation of DNA sequences. *Myotis lucifugus* and *M. septentrionalis* recently have been reported to occur near the Texas border in Oklahoma and Louisiana, respectively, and due to similarity of appearance, both species easily could be mistaken for *M. austroriparius*, a common inhabitant of East Texas. All three species co-occur across much of the southeastern United States. *Myotis septentrionalis* recently was listed under the Endangered Species Act as Endangered, and *M. lucifugus* has seen drastic reductions in abundance due to white-nose syndrome. Therefore, special care is needed when capturing any of these species due to the cryptic nature of their external morphology and the potential for misidentification in the field. The objective of this study was to determine if wing measurements obtained in the field could be used to differentiate among these three species. Measurements of 13 wing elements from 45 museum specimens were compared using univariate and multivariate statistics. Significant multivariate differences among species were detected, indicating that some wing characteristics may be effective for differentiation. These wing characteristics were compiled into a dichotomous key that researchers can use to easily identify species in the field. Using this technique, non-target species can be released quickly without harm, whereas individuals of species of interest can be confidently collected for scientific research.

Key words: cryptic species, *Myotis austroriparius*, *Myotis lucifugus*, *Myotis septentrionalis*, species identification, wing measurements, wing morphology

Introduction

By definition, cryptic species are difficult, if not impossible, to differentiate morphologically from one another (Mayr 1970). Many methods of differentiating among cryptic species have been established, including comparisons of cranial morphology or DNA sequences (Parkinson 1979; Mayer et al. 2007). However, these methods are invasive, often require euthanasia, and typically cannot be done quickly or in the field (Weller

et al. 2007). Such methods are not ideal when one or more species involved is a protected species. Moreover, researchers might choose not to collect species that are difficult to discern from protected species to avoid the possible repercussions of mistaken identification, including regulatory issues.

The Southeastern Myotis (*Myotis austroriparius*) is widely distributed across eastern Texas (Schmidly and Bradley 2016). The Northern Long-eared Bat (*Myotis septentrionalis*) has been reported throughout much of Louisiana, including areas near the Texas border (Stevens et al. 2017), and it is a protected species under the Endangered Species Act (United States Fish and Wildlife Service 2022). Further, recent reports indicate that the Little Brown Bat (*Myotis lucifugus*) occurs along the Oklahoma/Texas border (Roehrs et al. 2012). These three species are cryptic and difficult to distinguish morphologically. Although published distribution maps based on historical occurrences of these species do not show sympatry in Texas (Fig. 1; Fenton and Barclay 1980; Jones and Manning 1989; Caceres and Barclay 2000; Schmidly and Bradley 2016), niche models and recent distribution data suggest the potential

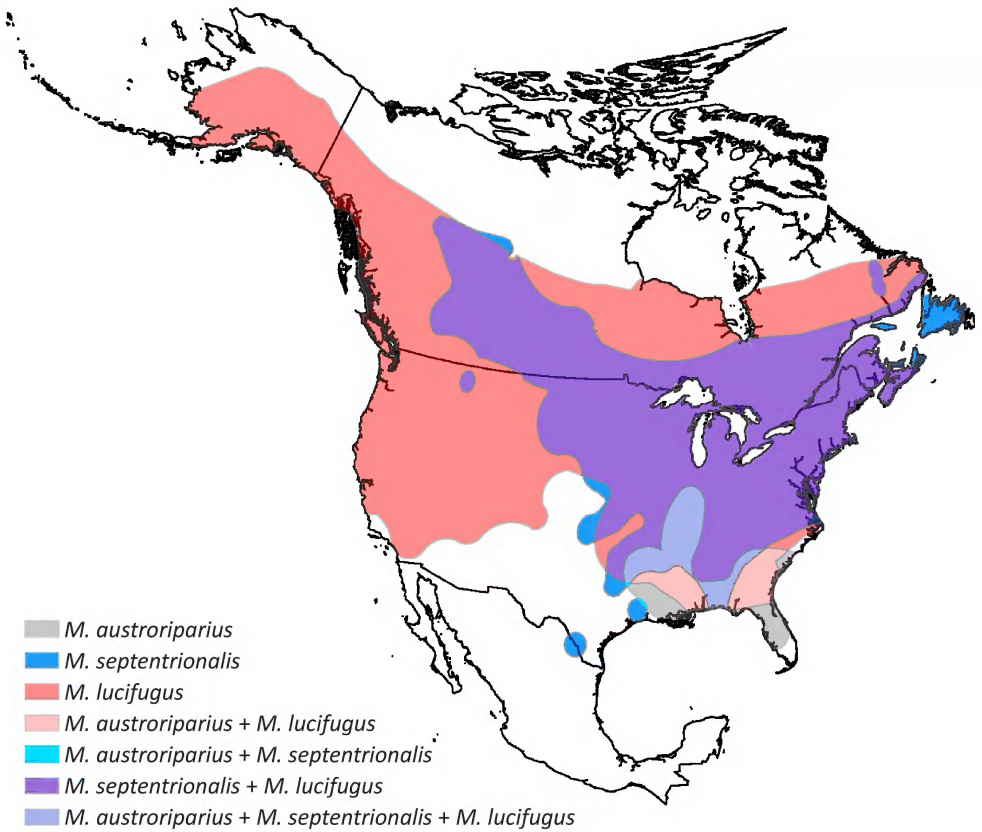
M. austroriparius
M. septentrionalis
M. lucifugus
M. austroriparius + M. lucifugus
M. austroriparius + M. septentrionalis
M. septentrionalis + M. lucifugus
M. austroriparius + M. septentrionalis + M. lucifugus

Figure 1. Geographic distributions of *Myotis austroriparius*, *M. septentrionalis*, and *M. lucifugus* highlighting co-occurrence in the southeastern portion of the United States.

for co-occurrence in northeastern Texas (Dixon 2011; Grimshaw et al. 2021; Roehrs et al. 2012; Schmidly and Bradley 2016; Stevens et al. 2017). Furthermore, these three species are sympatric across much of the southeastern United States. Because of their cryptic nature, misidentification of these taxa is possible. In fact, one published record of *M. lucifugus* in Texas was later identified as *M. austroriparius* (Schmidly et al. 2024). This correction was based on an analysis of skulls in an unpublished 1979 report of mammals from Big Thicket National Preserve (Schmidly et al. 2024) and highlights the need for noninvasive means of confidently identifying these three species in the field based on external characteristics.

Stevens et al. (2017) reported one characteristic that can be used to differentiate between *M. septentrionalis* and *M. austroriparius* in the field; the plagiopatagium of *M. septentrionalis* connects at the toe, whereas in *M. austroriparius* it connects at the ankle, although this can be difficult to determine in some individuals. However, no such character exists to differentiate *M. lucifugus* from either species, and additional morphological characteristics would be beneficial when confirming differences between *M. septentrionalis* and *M. austroriparius*. Stevens et al. (2017) emphasized that because the species are difficult to differentiate, it is possible *M. septentrionalis* has existed in Louisiana historically but was misidentified as *M. austroriparius*. Current data suggests a similar situation may occur in northeastern Texas because no guidance exists to differentiate among these three species. This potential sympatry in northeastern Texas reveals the necessity of a technique for differentiating the three species in the field.

Wing morphology varies among bat species (Bahlman et al. 2016) and can determine the habitats that bats forage in (Bullen and McKenzie 2001). Further, wing characteristics have proven useful in differentiating cryptic Old World bat species (Sun et al. 2008; Furman et al. 2010). Because the three species that are the focus of this study have different foraging ecologies, we hypothesized that wing measurements may vary significantly and could be useful in differentiating these species. *Myotis septentrionalis* primarily gleans insects off surfaces such as leaves, branches, and trunks of shrubs and trees (Caceres and Barclay 2000), whereas *M. austroriparius* and *M. lucifugus* are aerial insectivores that catch insects on the wing (Fenton and Barclay 1980; Jones and Manning 1989). In addition, *Myotis austroriparus* specializes in foraging over water (Jones and Manning 1989), whereas *M. lucifugus* is more general in its foraging behavior (Fenton and Barclay 1980). Thus, the goal of this study was to determine if differences in wing morphologies related to foraging strategies could serve as a means of noninvasive field identification of these three cryptic and sympatric, or potentially sympatric, *Myotis* species in the southeastern United States.

MATERIALS AND METHODS

Museum specimens were identified to species based on a combination of external (hair color and texture, attachment of uropatagium to foot or ankle) and cranial characteristics (size, degree to which braincase was domed). Adult specimens, as determined by the presence of fused epiphyses, of *M. septentrionalis* (9 males, 6 females), *M. austroriparius* (11 males, 6 females), and *M. lucifugus* (6 males, 7 females) were obtained from the Natural Science Research Laboratory (NSRL) of the Museum of Texas Tech University. All *M. austroriparius* and *M. septentrionalis* specimens were collected from Louisiana; *M. lucifugus* specimens had been collected primarily from the midwestern US, but all specimens were of the same subspecies (*M. l. lucifugus*) that would be expected to co-occur with *M. austroriparius* and *M. septentrionalis*. For each individual, 13 elements of the right wing (Fig. 2) were measured three times each by HB using a millimeter ruler, and the three replicates for each measurement were averaged. Differences in lengths of wing elements among treatment groups (i.e., species and sex) were tested using a multivariate analysis of variance (MANOVA) based on a Wilks-Lambda test statistic as well as univariate analyses of variance (ANOVA). Differences were illustrated based on a Discriminant Function Analysis (DFA).

Specimens examined (45).—*Myotis austroriparius* (17): USA: Louisiana; Natchitoches Parish (TTU 153675, 153676, 153677), Ouachita Parish

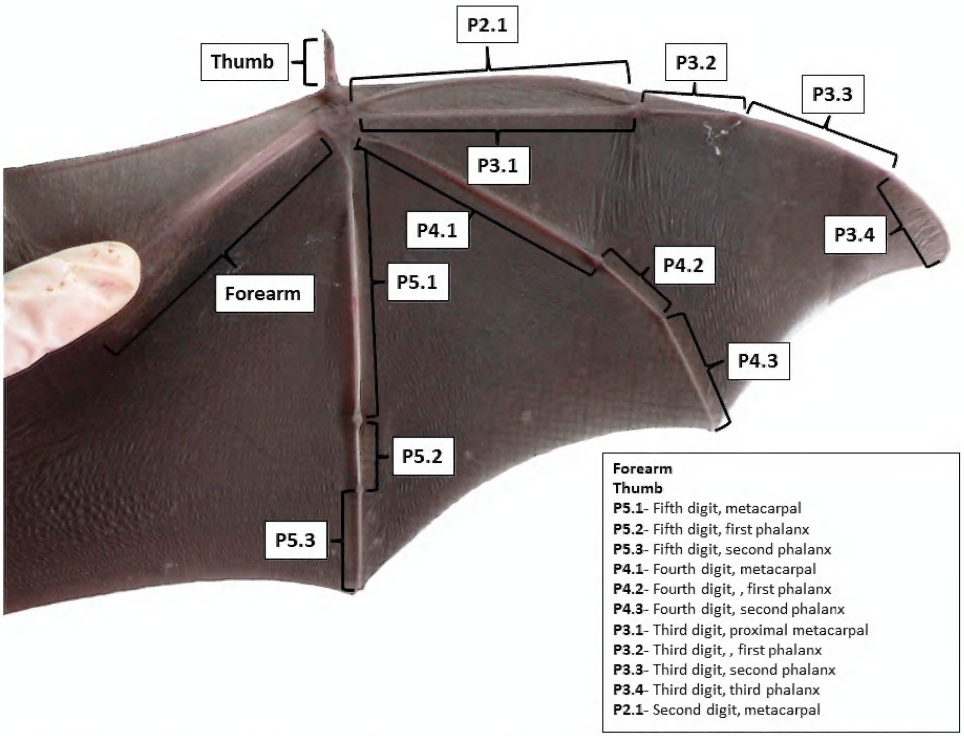

Figure 2. Illustration of the 13 wing elements employed in this study. The letter "P" is used to abbreviate "phalanx" with the first number indicating which phalanx (counting from the most lateral digit to the most medial digit, with the thumb as digit one) and the second number indicating which element on the phalanx (counting from the metacarpal to the most distal phalanx).

(TTU 153680), Rapides Parish (TTU 153720, 153722, 153723), Tangipahoa Parish (TTU 153732), West Feliciana Parish (TTU 153735, 153736, 153738, 153739, 153740, 153741, 153742, 153746), Winn Parish (TTU 155810). *Myotis lucifugus* (13): USA: Michigan; Kalamazoo County (TTU 139204, 139205, 139206); Minnesota; Hennepin County (TTU 16684, 16685), Houston County (TTU 16686), Itasca County (TTU 16687, 16688, 16689), Lake County (TTU 17863), Wright County (TTU 16690); Ohio, Hamilton County (TTU 242); Tennessee, Campbell County (TTU 7544). *Myotis septentrionalis* (15): USA: Lousiana; East Feliciana Parish (TTU 145888), Grant Parish (TTU 145889), Jackson Parish (TTU 130150, 131156, 145890, 145891, 145892), West Feliciana Parish (130149, 131453, 153758, 153759, 153760, 153761, 153762, 158664).

RESULTS

Species and sexes were variable regarding the 13 wing characteristics (Table 1). Multivariate analysis of variance indicated a highly significant difference among species but no significant difference between sexes. In addition, there was no significant species by sex interaction (Table 1), indicating that the differences

Table 1. Results from MANOVA (Multivariate Difference) and ANOVA conducted on each of the 13 wing elements separately to examine differences between species, sexes, and their interaction.

	M. austroriparius		*M. lucifugus*		*M. septentrionalis*						
	Females	Males	Females	Males	Females	Males	Factor	df	MS	F-Ratio	P-value
					Multivariate Differences						
							Species	26		10.06	<0.001
							Sex	13		1.04	0.448
							Interaction	26		0.76	0.774
					Forearm Length						
Mean	36.72	36.05	35.91	35.47	33.69	33.13	Species	2	35.45	35.59	<0.001
SD	0.66	1.38	0.78	1.37	0.63	0.58	Sex	1	3.35	3.36	0.075
N	6	11	7	6	6	9	Interaction	2	0.05	0.05	0.952
					Thumb length						
Mean	5.78	6.06	5.95	6.72	5.36	5.28	Species	2	3.60	7.41	0.002
SD	0.25	0.73	0.53	0.48	0.90	0.89	Sex	1	1.11	2.29	0.138
N	6	11	7	6	6	9	Interaction	2	0.62	1.28	0.289
					Second Metacarpel (P2.1)						
Mean	30.56	30.38	30.76	30.81	27.78	27.15	Species	2	47.73	35.01	<0.001
SD	0.93	0.90	1.16	0.85	1.48	1.51	Sex	1	0.69	0.51	0.482
N	6	11	7	6	6	9	Interaction	2	0.41	0.30	0.743
					Third Metacarpel (P3.1)						
Mean	33.03	32.50	32.67	32.19	29.94	29.54	Species	2	39.82	60.60	<0.001
SD	0.48	0.87	0.96	0.67	0.67	0.93	Sex	1	2.34	3.57	0.066
N	6	11	7	6	6	9	Interaction	2	0.01	0.02	0.980
					First Phalanx of Third Metacarpel (P3.2)						
Mean	11.06	10.94	11.57	11.53	10.78	10.50	Species	2	2.85	11.31	<0.001
SD	0.44	0.53	0.36	0.49	0.66	0.49	Sex	1	0.23	0.90	0.349
N	6	11	7	6	6	9	Interaction	2	0.05	0.20	0.821
					Second Phalanx of Third Metacarpel (P3.3)						
Mean	9.67	9.67	9.90	9.86	10.33	9.50	Species	2	0.28	0.43	0.657
SD	0.28	0.60	0.70	0.68	0.59	1.34	Sex	1	0.91	1.41	0.243
N	6	11	7	6	6	9	Interaction	2	0.79	1.23	0.305

Table 1. (cont.)

	M. austroriparius		*M. lucifugus*		*M. septentrionalis*						
	Females	Males	Females	Males	Females	Males	Factor	df	MS	F-Ratio	P-value
					Third Phalanx of Third Metacarpel (P3.4)						
Mean	7.36	7.15	5.79	5.89	6.47	6.44	Species	2	7.21	10.62	<0.001
SD	0.78	0.91	0.51	0.69	0.46	1.12	Sex	1	0.02	0.03	0.860
N	6	11	7	6	6	9	Interaction	2	0.09	0.13	0.879
					Fourth Metacarpel (P4.1)						
Mean	32.36	31.94	31.62	31.28	29.72	28.94	Species	2	31.57	46.69	<0.001
SD	0.48	0.89	1.04	0.68	0.52	0.95	Sex	1	2.81	4.16	0.048
N	6	11	7	6	6	9	Interaction	2	0.19	0.28	0.757
					First Phalanx of Fourth Metacarpel (P4.2)						
Mean	8.89	8.88	9.48	9.22	8.11	7.72	Species	2	7.40	51.71	<0.001
SD	0.14	0.51	0.37	0.36	0.38	0.30	Sex	1	0.51	3.52	0.068
N	6	11	7	6	6	9	Interaction	2	0.14	0.97	0.390
					Second Phalanx of Fourth Metacarpel (P4.3)						
Mean	10.31	10.11	10.24	10.03	10.61	10.00	Species	2	0.10	0.23	0.794
SD	0.65	0.36	0.64	0.43	0.66	0.91	Sex	1	1.23	2.77	0.104
N	6	11	7	6	6	9	Interaction	2	0.20	0.44	0.645
					Fifth Metacarpel (P5.1)						
Mean	32.03	31.15	30.86	30.83	29.81	28.94	Species	2	18.79	23.73	<0.001
SD	0.37	0.98	1.01	0.96	0.46	1.05	Sex	1	3.67	4.64	0.038
N	6	11	7	6	6	9	Interaction	2	0.81	1.02	0.371
					First Phalanx of Fifth Metacarpel (P5.2)						
Mean	8.69	8.59	8.98	8.81	8.11	7.89	Species	2	2.95	19.83	<0.001
SD	0.37	0.45	0.39	0.26	0.43	0.34	Sex	1	0.29	1.96	0.169
N	6	11	7	6	6	9	Interaction	2	0.01	0.09	0.915
					Second Phalanx of Fifth Metacarpel (P5.3)						
Mean	9.00	8.52	8.14	8.33	10.17	8.72	Species	2	5.02	8.75	<0.001
SD	0.51	0.35	0.95	1.08	0.77	0.84	Sex	1	3.58	6.24	0.017
N	6	11	7	6	6	9	Interaction	2	2.32	4.04	0.025

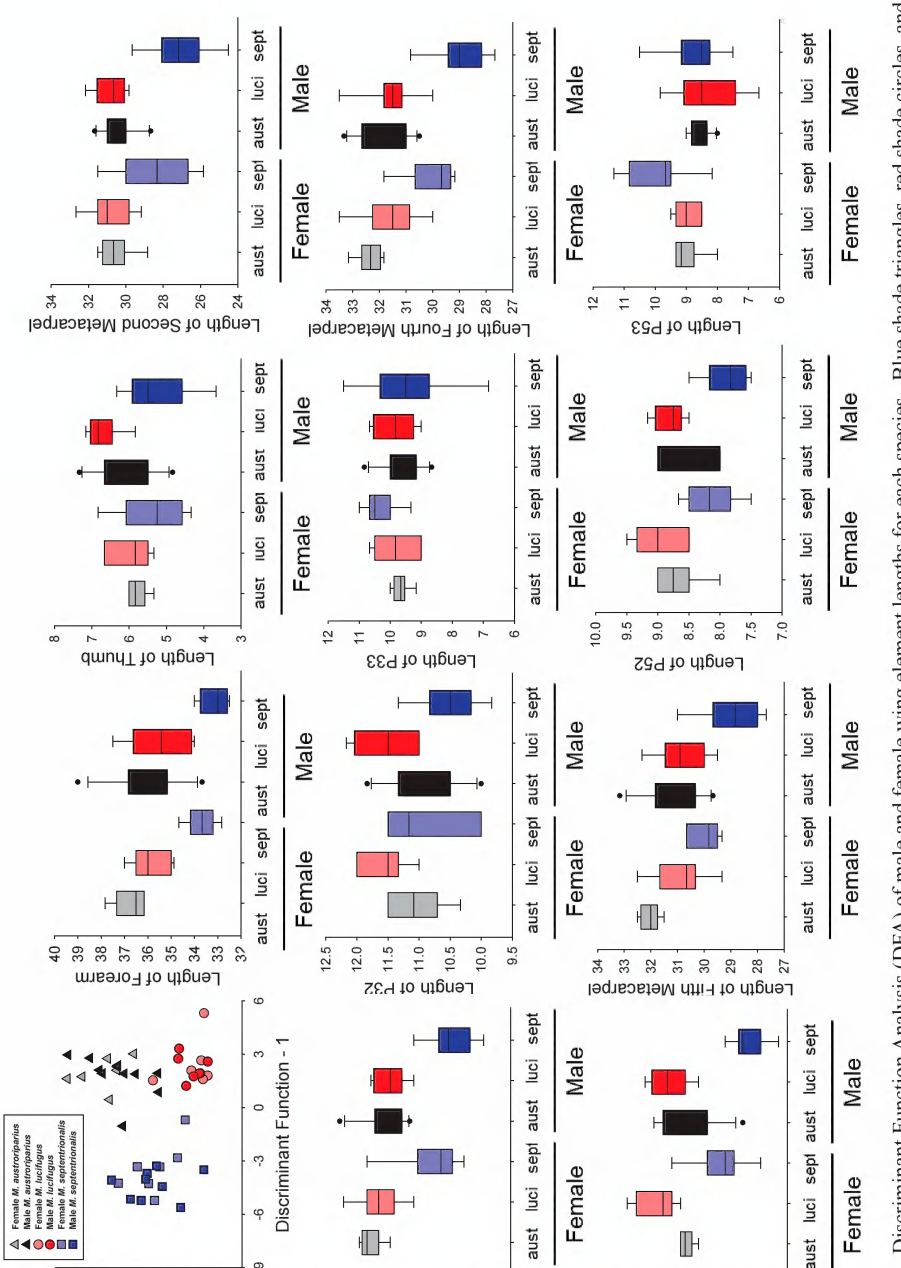

Figure 3. Discriminant Function Analysis (DFA) of male and female wing element lengths for each species. Blue shade triangles, red shade circles, and gray shade squares represent *M. austroriparius*, *M. lucifugus*, and *M. septentrionalis*, respectively. Light shades represent females and dark shades represent males. Box plots for wing elements with no overlap between at least two groups. All measurements are in millimeters.

among species were not dependent on sex. Results from DFA illustrate these differences (Fig. 3). Univariate ANOVA's indicated significant differences among species in the lengths of all elements except P3.3 and P4.3 (Table 1). The forearm, P4.1, P4.2, P5.1, and P5.3 also exhibited significant differences between the sexes. There was a significant univariate species by sex interaction for P5.3.

Although no wing element showed zero overlap in measurements among all three species and two sexes, many elements exhibited no overlap between two species (Fig. 3; Table 1). There was no overlap between *M. austroriparius* and *M. lucifugus* females for P3.4 (0.28 mm difference) and P4.2 (0.08 mm difference); for males, all characters overlapped for these species. Between *M. lucifugus* and *M. septentrionalis* females, there was no overlap for forearm (0.81 mm difference), P2.1 (0.34 mm difference), P3.1 (1.10 mm difference), P4.1 (0.34 mm difference), P4.2 (0.62 mm difference), P5.2 (0.05 mm difference), and P5.3 (0.31 mm difference); for males there was no overlap for forearm (0.39 mm difference), thumb (0.07 mm difference), P2.1 (1.3 mm difference), P3.1 (1.05 mm difference), P3.2 (0.05 mm difference), P4.1 (0.71 mm difference), P4.2 (0.84 mm difference), and P5.2 (0.32 mm difference). Between *M. austroriparius* and *M. septentrionalis* females, there was no overlap for the forearm (1.74 mm difference), P2.1 (0.34 mm difference), P3.1 (1.10 mm difference), P4.1 (1.64 mm difference), P4.2 (0.26 mm difference), and P5.1 (1.39 mm difference); for males, there was no overlap in the forearm (0.96 mm difference), P2.1 (0.82 mm difference), P3.1 (1.16 mm difference), P4.1 (1.16 mm difference), P4.2 (0.35 mm difference), and P5.1 (0.18 mm difference).

Based on these data, a dichotomous key was developed to aid researchers in differentiating these species in the field (Table 2). These sequential guidelines for differentiation begin with the identification of the individual's sex. For males, differentiation should begin with P3.1. If this measurement is less than 31 mm, it is likely *M. septentrionalis*, but this can be further confirmed by measurements of less than 29 mm for P2.1 and less than 30 mm for P4.1, because both *M. austroriparius* and *M. lucifugus* are significantly

Table 2. Dichotomous key to differentiate *Myotis septentrionalis*, *M. lucifugus*, *M. austroriparius* using wing measurements.

1. Determine the sex.
    a. Male: Go to 2.
    b. Female: Go to 4.
2. Measure P3.1.
    a. Less than 31 mm: *M. septentrionalis* (confirm P2.1 is less than 29 mm and P4.1 is less than 30 mm)
    b. 31 mm or greater: Go to 3.
3. Measure P3.4 and P3.2*
    a. P3.4 less than 6.5 mm and P3.2 greater than 11.25 mm: *M. lucifugus*
    b. P3.4 greater than 6.5 mm and P3.2 less than 11.25 mm: *M. austroriparius*
4. Measure Forearm.
    a. Less than 35 mm: *M. septentrionalis* (for further confirmation, the lengths of P3.1, P4.1, and P5.1 should each be less than 31 mm).
    b. 35 mm or greater: Go to 5.
5. Measure P3.4.
    a. Less than 6.5 mm: *M. lucifugus*.
    b. 6.5 mm or greater: *M. austroriparius*.

*It should be noted that male *M. austroriparius* and male *M. lucifugus* cannot be confidently distinguished since no measurements were found to have a significant difference without some level of overlap.

larger in these elements. If P3.1 is 31 mm or greater, measurements of P3.4 and P3.2 can be used in conjunction to differentiate *M. lucifugus* and *M. austroriparius*. Because all significant differences demonstrated some level of overlap between males of these species, it is recommended to use these two elements that exhibit the least overlap absolutely. Additionally, these elements exhibit proportionately small overlap relative to the average element length. In the case of *M. lucifugus*, the species can be differentiated by a P3.4 less than 6.5 mm in combination with a P3.2 greater than 11.25 mm. Conversely, *M. austroriparius* should possess a P3.4 greater than 6.5 mm and P3.2 less than 11.25 mm. Use of these two measurements in tandem offers researchers a reasonably sound method for discerning the species in the field.

When differentiating females, it is recommended to begin with the forearm. If the forearm is less than 35 mm, the species is likely *M. septentrionalis*. For further confirmation, the lengths of P3.1, P4.1, and P5.1 should each be less than 31 mm. However, if the forearm is greater than 35 mm, then P3.4 can be used to differentiate *M. austroriparius* from *M. lucifugus*. If P3.4 is less than 6.5 mm, the species can be identified as *M. lucifugus*.

DISCUSSION

Because identification of cryptic species typically relies on invasive procedures such as extraction and examination of crania or generation of DNA sequences, unprotected species often are not collected out of caution when they are cryptic with those with protected status. Our research identified characteristics of wing morphology that could be used in the field to differentiate *M. austroriparius* and *M. lucifugus* from the cryptic and endangered species *M. septentrionalis*. Properly identifying protected cryptic species is crucial to their conservation, especially when they overlap in their geographic distributions, such as the three species addressed here that potentially overlap in the southeastern United States. Use of external wing measurements is a less invasive and often overlooked alternative to cranial morphology and DNA testing. This methodology will help researchers in the field to quickly differentiate *M. septentrionalis*, *M. austroriparius*, and *M. lucifugus*.

Differences between sexes also were examined to account for this effect when examining differences among species. Sexual dimorphism is common in the genus *Myotis* (Stevens and Platt 2015). One common explanation for larger female size is the Big Mother Hypothesis (Stevens et al. 2013) that suggests that females overcome the extra burden of reproduction due to added weight gain by having larger body sizes and in particular larger wing elements. Although the multivariate difference between sexes was nonsignificant, univariate differences were significant for a number of wing elements when examined separately. Based on these univariate differences, sizes were typically larger for females than for males.

It should be noted that because the wings of *Myotis* are small, significant differences among species regarding wing elements are absolutely small as well, but in some cases share no overlap between species. These differences provide a reliable guide for differentiating these three species because average lengths of *M. septentrionalis* wing elements were in general significantly smaller. In particular, differences were fairly reliable among the males of each species. The smaller sample size of females included in this study likely led to the less-pronounced differences among species for this sex.

It should be noted that these results can only be applied to the subspecies *M. l. lucifugus*, as this is the only subspecies sampled in this study and the only subspecies which would co-occur with *M. septentrionalis* and *M. austroriparius*. The results from this study, however, can be assumed to be applicable to all areas of the US where there is known or suspected sympatry of these three *Myotis* species. Despite our ability to detect significant differences among species, a larger sample size for each group, especially females, likely would provide more precise estimates of differences. Regardless, the data herein describe significant differences that may be applied in the field as a relative guide to differentiating among the three species without invasive DNA testing or cranial measurements.

Additionally, the effectiveness of using wing morphology to differentiate these cryptic species suggests that this technique might have utility in identifying other cryptic species, enabling bats of concern to be quickly identified and released after capture and species of research interest to be retained. As previously mentioned, differences in foraging behavior often translate into phenotypic differences (Bullen and McKenzie 2001). In the case where cryptic species differ in foraging behavior, wing morphology may provide a useful perspective from which to begin to examine diagnostic differences. Such an approach may have a more general application than just the three species examined in this study.

In conclusion, our data demonstrate statistical differences among the wing morphologies of *M. septentrionalis*, *M. austroriparius*, and *M. lucifugus* that can be used to differentiate among the three species in the field rather than more invasive approaches such as preparing and examining individuals as museum specimens or consideration of molecular data from tissue samples. No single measurement can be used to confidently differentiate all three species; however, examining a combination of measurements in the field could prove very useful in identifying species. Methods for identifying cryptic species in the field, such as that described herein, are vitally important to research, because they allow regulatory agencies to permit collecting in areas where it might otherwise be curtailed due to concerns of inadvertently collecting protected species.

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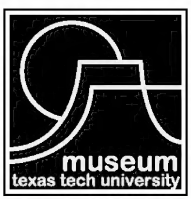

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